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Alexandria Lynn Pivovaroff
University of California, Riverside

Cheryl Swift
Whittier College

Loretta L. Battaglia
Southern Illinois University at Carbondale

Brittany Kunz
Whittier College

William J. Platt
University of California, Riverside

See next page for additional authors

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Authors

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Physiological Profiles as Indicators of Response to Hurricane Disturbance for Three Coastal Wetland Species

Alexandria Lynn Pivovarov^{†*}, Cheryl Swift[‡], Loretta L. Battaglia[§], Brittany Kunz[‡], William J. Platt^{††}, Carrie L. Yoder^{††**}

[†]Department of Botany & Plant Sciences
University of California Riverside
Riverside, CA 92521, U.S.A.

[§]Department of Plant Biology & Center for Ecology
Southern Illinois University Carbondale
Carbondale, IL 62901, U.S.A.

[‡]Department of Biology
Whittier College
Whittier, CA 90608, U.S.A.

^{††}Department of Biological Sciences
Louisiana State University
Baton Rouge, LA 70803, U.S.A.

ABSTRACT

Pivovarov, A.L.; Swift, C.; Battaglia, L.L.; Kunz, B.; Platt, W.J., and Yoder, C.L., 2015. Physiological profiles as indicators of response to hurricane disturbance for three coastal wetland species. *Journal of Coastal Research*, 31(4), 986–993. Coconut Creek (Florida), ISSN 0749-0208.

Hurricanes alter light and water availability *via* canopy damage and storm surge delivery and are expected to intensify with climate change. Plant species respond to environmental changes by making physiological adjustments *in situ* or through distribution changes. Three years after Hurricane Katrina, we compared functional traits and water relations among three species along the coenocline at Weeks Bay National Estuarine Research Reserve, Fairhope, Alabama, U.S.A. Based on posthurricane distribution changes for these species, we hypothesized that (1) *Cladium mariscus*, whose distribution expanded slightly, is responsive to increased light availability in the disturbed forest at the landward end but is strongly limited by water stress at its seaward edge; (2) *Baccharis halimifolia*, whose distribution shifted and abundance increased posthurricane, is responsive to increased light availability, cannot tolerate very low light levels or water logged soils, but can tolerate moderate salinity; and (3) *Morella cerifera*, whose distribution remained unchanged, would show little or no difference in measured functional traits and water relations at its landward *vs.* seaward edges. *Cladium mariscus* showed decreased water potential (Ψ) at its seaward edge, but leaf mass per area (LMA) did not vary as forest cover increased landward. *Baccharis halimifolia* exhibited lowest LMA and highest Ψ in the middle of its distribution, but was least vulnerable to cavitation (Ψ_{50}) with increased forest cover. *Morella cerifera* exhibited no difference in water stress, wood density, or Ψ_{50} across its distribution. Our results suggest differences in physiological response to light availability and water stress may affect the postdisturbance distribution of plant species and influence changes in distribution of species exposed to chronic sea level rise.

ADDITIONAL INDEX WORDS: Leaf mass per area, stomatal conductance, water potential, plant migration, sea level rise, Hurricane Katrina.

INTRODUCTION

The coastal transition bridging marine to terrestrial ecosystems is an ecological vanguard of global climate change impacts (Brinson, Christian, and Blum, 1995; Conner and Inabinette, 2003; Craft *et al.*, 2009; McLeod and Ciravolo, 1997; Scavia *et al.*, 2002; Warrick *et al.*, 1995). Along the coast, sea level rise (SLR) and shifts in tropical storm regimes due to climate change have the potential to dramatically affect the distribution of biota across these transitional ecosystems. The combined effects of SLR and altered storm regimes involve gradual and chronic background changes in sea level, punctuated by abrupt but ephemeral, large changes in sea level as powerful hurricanes make landfall along low-lying coastlines (Daniels 1992). Along the northern Gulf of Mexico, coastal ecosystems are already experiencing the impacts of SLR (Battaglia *et al.*, 2012; Shirley and Battaglia, 2006), the rate

of which is expected to increase in the coming decades (IPCC 2014). Tropical storms are predicted to decrease in frequency but intensify in this region throughout the 21st century (Bender *et al.*, 2010; Blake, Landsea, and Gibney, 2011), delivering massive storm surges farther inland. Intensified tropical storms will drive changes in light and water availability to plants (Bianchette *et al.*, 2009; Guntenspergen *et al.*, 1995) with delivery of storm surges and attendant wrack deposition (Blake, Landsea, and Gibney, 2011; Platt, Joseph, and Ellair, 2014; Tate and Battaglia, 2013), salt burning (Cahoon, 2006; Lam *et al.*, 2011), and wind-driven damage to forest canopies (Lam *et al.*, 2011; Rodgers, Murrah, and Cooke, 2009). The ability of species to cope with these changing conditions and/or migrate to more appropriate habitat is poorly understood.

Species in the ecological crosshairs of these climate change-driven disturbances may respond by making physiological adjustments *in situ* or through distributional changes, whether expanding, contracting, or shifting their range (Brinson, Christian, and Blum, 1995; Craft *et al.*, 2009; Donnelly and Bertness, 2001; Williams *et al.*, 1999). However, the pattern and direction of response will be determined by the species'

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*Corresponding author: alexandria.pivovarov@email.ucr.edu

**Deceased

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Figure 1. Weeks Bay NERR permanent transect elevations, salinity, and communities. Grey bars represent sampled community locations along the transect (FW = freshwater; SE = sparse ecotone; DE = dense ecotone; SF = seep forest; MF = mesic forest). Closed triangles represent elevations along the transect measured relative to mean sea level (msl). Open circles represent mean salinity of five measurements along the transect, measured 30 cm into the soil in June 2002. Closed circles represent mean salinity of five measurements made along the transect in 100-m² plots, measured 30 cm into the soil in June 2006, 9 mo after Hurricane Katrina.

physiological tolerance to abiotic factors, as well as competitive ability with co-occurring species (Crain *et al.*, 2004; Ervin and Wetzel, 2002; Kim, Cairns, and Bartholdy, 2011). Functional traits are an excellent approach to determine how species interact with their environment and with each other (Diaz and Cabido, 2001) because these traits influence organismal performance and capture trade-offs and because there is more variation between species than within species (McGill *et al.*, 2006; Westoby and Wright, 2006). For example, leaf mass per area (LMA), *i.e.* the ratio of leaf dry mass to leaf area, is an anchor trait in the leaf economics spectrum and is associated with leaf life span, leaf nutrient concentration, and gas exchange rates (Wright *et al.*, 2004). LMA is also shown to vary strongly with respect to light, as a higher ratio of leaf area to leaf biomass (a lower LMA) results in a larger, thinner surface to intercept light in low-light conditions, whereas a higher ratio of leaf biomass to leaf area (a higher LMA) can increase photosynthetic capacity in high-light conditions (Poorter *et al.*, 2009). Wood density is another functional trait, and is associated with trade-offs in growth rate (Enquist *et al.*, 1999; Loehle, 1988; Muller-Landau, 2004; Roderick, 2000), branch mechanical strength (Niklas, 1992), and resistance to drought-induced xylem cavitation (Hacke *et al.*, 2001; Maherali, Pockman, and Jackson, 2004; Sperry, 2003). Additionally, water relations concern essential functions for plants related to the capture, movement, and control of water within the plant and is coordinated with the photosynthetic systems of plants (Brodribb, 2009; Santiago *et al.*, 2004) and, therefore, is associated with productivity and drought adaptation. Hence, assessing plant responses to the environment through the study of functional traits and water relations is common (Baraloto *et al.*, 2010; Pivovarov *et al.*, 2014; Santiago and Wright, 2007; Sterck *et al.*, 2011), but few studies have linked these traits to hurricane disturbance responses, although these disturbances are often large and can have a significant effect on

a system. For example, strong winds resulting in canopy damage can enhance light levels for understory species and potentially lead to physiological changes, such as altered LMA or increased stomatal conductance, and distribution expansions, as previously light-limited species colonize (Fruchter, 2012; Pickens and Hester, 2011; Shirley and Battaglia, 2006). Storm surges often flood and salinize soils, leading to altered plant–water relations and reduced growth rate and, potentially, driving contractions in distributions for species unable to tolerate those stresses (Conner and Inabinette, 2003; McLeod and Ciravolo, 1997; Munns, 2002).

In 2004, Hurricane Ivan, a Category 3 storm, which produced strong winds and a wave-driven storm surge, made landfall along the Alabama/Florida Panhandle coast line (Blake, Landsea, and Gibney, 2011) leading to reduction of forest cover by more than 40% in some areas along the Gulf Coast (Bianchette *et al.*, 2009). The following year, Hurricane Katrina, the third most intense storm on record (Blake, Landsea, and Gibney, 2011), produced winds and a strong storm surge that further altered vegetation cover (Lam *et al.*, 2011). These two intense hurricanes increased salinity levels and reduced vegetation cover along the coastal gradient at our study site, Weeks Bay National Estuarine Research Reserve (NERR), in coastal Alabama (Lam *et al.*, 2011; Rodgers, Murrah, and Cooke, 2009; Figure 1). The primary objective of our study was to characterize and compare the physiological profiles using functional traits and water relations of three common, dominant species, *Cladium mariscus* (L.) Pohl ssp. *jamaicense* (Crantz) Kük, *Baccharis halimifolia* L., and *Morella cerifera* L., which varied in their distributional breadth and responses along the coastal coenocline at Weeks Bay NERR following the Hurricanes Ivan and Katrina (Figure 2). We asked, “Can plant functional traits and water relations explain the postdisturbance distribution of these species?” To address our question, we examined plant functional traits (LMA and wood density) and water relations (xylem vulnerability to cavitation, diurnal water potentials, and diurnal stomatal conductance) for these species along a permanent transect that spans changes in salinity, soil water availability, and light availability with increasing elevation above mean sea level (msl; Figure 1). Water stress may be driven by flooded soils in the lower elevations of the transect, salinity in the midelevations, and low water availability in the high elevations (Figure 1). *Morella cerifera* was broadly distributed before the hurricanes and did not exhibit distributional or abundance shifts following the storms (Figure 2A). We hypothesized *M. cerifera* is not light limited and is able to tolerate water limitation resulting from drought, salinity, or waterlogged soils, and so, would show little difference in measured functional traits and water relations at its landward *vs.* seaward edge. Given that *B. halimifolia* greatly expanded its distribution landward and increased in abundance, with only a slight contraction at its seaward edge (Figure 2B), we hypothesized that it is responsive to increased light availability, cannot tolerate very low light levels or water logged soils, but can tolerate moderate salinity. Hence, it would show differences in trait values between its seaward and landward edges. *Cladium mariscus* had the narrowest distribution, and its range expanded only slightly at its landward edge with no

Figure 2. (A, top panel) Distribution of *Morella cerifera*, (B, middle panel) *Baccharis halimifolia*, and (C, bottom panel) *Cladium mariscus*, represented as the percentage of vegetation plots spanning the elevation gradient in which each species occurred. Plots were established in 2003, stratified by elevation zone, and censused annually until 2008.

abundance changes, so we hypothesized it is slightly responsive to light availability, but strongly limited by water stress. Therefore, *C. mariscus* would show major differences in functional traits and water relations at its range edges. Comparing functional traits across the seaward to landward distribution of a species may indicate the direction of response to ephemeral disturbances and improve our ability to predict future shifts of coastal wetland species in response to more permanent environmental change.

METHODS

This study used portions of a 400 m permanent transect established in June 2002, before the hurricanes, at Weeks Bay NERR, located 64 km SE of Mobile, Alabama, U.S.A.. The transect starts in brackish marsh, adjacent to a tidal creek that discharges into Weeks Bay. As the transect extends inland with attendant increases in elevation above msl, there is compositional turnover in the plant community and increased dominance of woody species and canopy cover (Figure 1). In 2003, five 100-m² plots were established within each of the elevation zones paralleling the transect. Plots were censused annually from 2003 to 2008 to track species distributions and abundance across the gradient (Figure 2). We focused our study in five plant communities that were traversed by the transect: the freshwater marsh, sparse shrub-marsh ecotone, dense shrub-marsh ecotone, wetland seep forest, and mesic forest (Figure 1). In 2002 (before the hurricanes) and 2006 (after the hurricanes), salinity was measured at depths of 30 cm with an Aquateer EC 300 salinity meter at 10-m intervals along the transect (Figure 1). The

Figure 3. Diurnal photosynthetically active radiation ($\mu\text{mol m}^{-2} \text{s}^{-1}$) measured at five sites along a 400-m permanent transect at the Weeks Bay NERR in July 2008. Errors bars represent the standard error of the mean.

forested communities sustained heavy canopy damage from the hurricanes and remained highly disturbed with partially open canopy at the time of this study (July 2008–June 2009). Our study species included *Morella cerifera*, a woody, evergreen shrub or tree that occurred in all five study communities, *Baccharis halimifolia*, a woody evergreen shrub or small tree that occurred in the sparse ecotone, dense ecotone, and seep forest, and *Cladium mariscus*, a dominant sedge that occurred in the freshwater marsh, sparse ecotone, and dense ecotone. For all measured traits, we sampled three to five individuals of the study species in each community in which they occurred. All traits were measured in July 2008, with the exception of xylem vulnerability to cavitation, which was measured in late June 2009.

LMA (g cm^{-2}) was determined by measuring a one-sided area of excised leaf samples with an area meter (LI-3100, Li-Cor Biosciences, Lincoln, Nebraska, U.S.A.). The leaves were then dried in an oven at 70°C for 48 hours and then weighed to determine dry leaf mass. LMA was calculated using leaf mass (g) divided by leaf surface area (cm^2).

Diurnal leaf water potential (Ψ , MPa) was measured using a pressure chamber (Model 1000, Plant Moisture Stress Instruments, Albany, Oregon, U.S.A.) to determine plant water status. Shoot samples were collected, bagged, and placed in a cooler before being transported back to the field station for measurement. Time from collection to measurement was approximately 30 to 45 minutes. Measurement times were approximately 0400, 0700, 0900, 1200, 1500, and 1800.

Diurnal stomatal conductance (g_s , $\text{mmol m}^{-2} \text{s}^{-1}$) was measured on fully mature leaves with an AP4 porometer (Dynamax Inc., Houston, Texas, U.S.A.), concurrently with water potentials (see above) to determine coordination of gas exchange with plant water status. The AP4 porometer has a light sensor on the sensor head/leaf clip from which diurnal photosynthetically active radiation (PAR; $\mu\text{mol m}^{-2} \text{s}^{-1}$) measurements were simultaneously taken (Figure 3).

Wood density for *M. cerifera* and *B. halimifolia* was measured by first removing the bark and pith from a fresh stem subsample approximately 10 to 15 mm long, then determining fresh volume (cm^3) of the sample using the water

Figure 4. Leaf mass per area for *Morella cerifera*, *Baccharis halimifolia*, and *Cladium mariscus* at five sites along a 400-m permanent transect at the Weeks Bay NERR in July 2008. Errors bars represent the standard error of the mean. Letters in common indicate no statistical difference ($p > 0.05$).

displacement method (Osazuwa-Peters, Zanne, and PrometheusWiki contributors, 2011; Williamson and Wiemann, 2010) by attaching the sample to a needle and immersing the sample in a beaker of water that is on a balance, and finally drying the sample for 48 hours at 75°C and determining dry mass (g). Wood density was measured as the ratio of dry mass to fresh volume (g cm^{-3}).

Vulnerability curves for *M. cerifera* and *B. halimifolia* were determined using the air injection method with a cavitation chamber (Plant Moisture Stress Instruments) (Sperry and Saliendra, 1994) to determine drought tolerance in late June 2009. Stems 5 to 8 mm in diameter from three individuals of each species at each site were cut under water in the field, wrapped in wet paper towels, doubled bagged, and placed in a cooler for transport to the laboratory. Samples were prepared by cutting stems under water to 14.2 cm, which is the same sample length used with the static rotor design for vulnerability curves generated from centrifugation, with the ends cleanly shaven by a razor blade. In our hydraulics line, we used a solution of filtered (0.2 μm) degassed water adjusted to 2 pH to prevent microbial growth in the line. To determine maximum hydraulic conductance (K_{max}), samples were flushed at 100 kPa for 20 minutes to remove embolisms. Stems were then placed on the hydraulics line with water flowing gravimetrically from an elevated source and through the stem. Flow rate was determined using three preweighed vials containing tissue to collect water at the exposed distal end of a stem for 10 seconds each. The vials were then reweighed to calculate flow (F), which was then used with the pressure head of the water (P ; approximately 3 KPa) to calculate hydraulic conductance (K):

$$K = \frac{F}{P} \quad (1)$$

Stem samples were then placed in the cavitation chamber, which used positive air pressure to induce embolisms by air seeding. Pressure was increased in steps of 0.5 and 1.0 MPa until the stem experienced 95% loss of hydraulic conductance.

For each step, the stem was under pressure for 20 minutes, then allowed to equilibrate for 15 minutes before hydraulic conductance was measured as previously described. Vulnerability curves were constructed using maximum hydraulic conductance to calculate the percentage of loss of hydraulic conductance (PLC) for each pressure step and then plotting water potential vs. the PLC:

$$PLC = \left[1 - \left(\frac{K}{K_{\text{max}}} \right) \right] \times 100 \quad (2)$$

Data for the vulnerability curves were fitted to a Weibull distribution:

$$PLC = \frac{100}{1 + \exp[a(\psi - b)]} \quad (3)$$

where ψ is water potential, and a and b are constants, using SAS 9.3 software (SAS Institute Inc., Cary, North Carolina, U.S.A.) (Pammenter and Willigen 1998). ψ_{50} was calculated as the pressure at which the stem experienced 50% loss of hydraulic conductance.

We used one-way analysis of variance (ANOVA; SAS 9.3) to test for differences in LMA, predawn and midday xylem water potentials, ψ_{50} , and xylem density within location across species and within species across location. We used one-way ANOVA instead of two-way ANOVA because not all species occurred at all locations. We used Tukey's posthoc test, and the type I error was set at 0.05.

RESULTS

LMA was not significantly different for *C. mariscus* over its entire range of occurrence from the freshwater marsh to the dense ecotone (Figure 4). *Baccharis halimifolia* LMA was greatest in the sparse ecotone and lowest in the dense ecotone ($p < 0.05$; Figure 4). *Morella cerifera* LMA was not significantly different in the freshwater marsh, sparse ecotone, and dense ecotone, but it decreased in the seep forest and mesic forest ($p < 0.05$; Figure 4), demonstrating a shift in leaf morphology in the more light-limited environment (Figure 3). Within each community, *C. mariscus* had the highest LMA of all co-occurring study species ($p < 0.05$). Only in the dense ecotone, which is midrange for the distributions of both *M. cerifera* and *B. halimifolia*, was LMA of these two species significantly different from each other ($p < 0.05$; Figure 4).

Predawn water potentials for *C. mariscus* were lowest in the freshwater marsh ($p < 0.05$; Figure 5). There were no significant differences in predawn water potentials among communities for *B. halimifolia*. Predawn water potentials for *M. cerifera* were significantly more negative in the freshwater marsh ($p < 0.05$; Figure 5). Within communities, there was no significant difference for predawn water potentials among co-occurring species (Figure 5). Midday water potentials for *C. mariscus* were lowest in the freshwater marsh ($p < 0.05$), following the pattern of its predawn water potentials (Figure 5). *Baccharis halimifolia* midday water potentials were least negative in the dense ecotone, which was statistically different from the sparse ecotone and seep forest zones ($p < 0.05$; Figure 5). *Morella cerifera* midday water potentials did not differ among communities. Within communities, *C. mariscus* had the most negative midday water potentials of all co-occurring study

Figure 5. Diurnal water potentials (left) and diurnal stomatal conductance (right) for *Morella cerifera*, *Baccharis halimifolia*, and *Cladium mariscus* measured at five sites along a 400-m permanent transect at the Weeks Bay NERR in July 2008. Errors bars represent the standard error of the mean.

species ($p < 0.05$). *Morella cerifera* had the least negative midday water potentials of all co-occurring study species ($p < 0.05$), but only in the seep forest were *B. halimifolia* and *M. cerifera* significantly different ($p < 0.05$; Figure 5).

In all communities it occurred, stomatal conductance for *C. mariscus* was highest during the morning (0700), ranging between 210 to 275 $\text{mmol m}^{-2} \text{s}^{-1}$, then steadily declined over the course of the day (Figure 5). Within the freshwater marsh, midday water potentials of *C. mariscus* were very negative but reverted back to values consistent with predawn measurements during the course the day (Figure 5). For *B. halimifolia*, stomatal conductance was highest in the morning (0900) in the sparse ecotone, where it decreased dramatically during midday (12:00; Figure 5). Conversely, *B. halimifolia* had its lowest morning (0900) stomatal conductance in the dense ecotone, where it increased during midday (1200; Figure 5). The overall lowest g_s for *B. halimifolia* was during the evening (1800) in the seep forest, which is likely due to light limitation. For *M. cerifera*, maximum stomatal conductance occurred midday (1200) in the sparse ecotone (Figure 5). Stomatal conductance for *M. cerifera* was always lowest in the mesic forest, where it is most likely light limited (Figure 5).

Figure 6. Wood density for *Morella cerifera* and *Baccharis halimifolia* at five sites along a 400-m permanent transect at the Weeks Bay NERR in July 2008. Errors bars represent the standard error of the mean. Letters in common indicate no statistical difference ($p > 0.05$).

Wood density did not differ among communities for *M. cerifera*. *Baccharis halimifolia* had lower wood density in the dense ecotone and seep forest than in the sparse ecotone ($p < 0.05$, Figure 6). Within communities, wood density differed between *M. cerifera* and *B. halimifolia* in the dense ecotone and seep forest ($p < 0.05$), but not in the sparse ecotone (Figure 6).

Xylem vulnerability to cavitation did not differ among communities for *M. cerifera* or *B. halimifolia* (Figure 7). Within communities, xylem vulnerability to cavitation was significantly greater for *B. halimifolia* than *M. cerifera* in the sparse ecotone and dense ecotone zones ($p < 0.05$) but not the seep forest (Figure 7).

DISCUSSION

As a species whose narrow distribution slightly expanded landward after hurricanes (Figure 2), we predicted that *C. mariscus* should be slightly responsive to increased light

Figure 7. Xylem vulnerability to cavitation (Ψ_{50}) for *Morella cerifera* and *Baccharis halimifolia* at five sites along a 400-m permanent transect at the Weeks Bay NERR in June 2009. Errors bars represent the standard error of the mean. Letters in common indicate no statistical difference ($p > 0.05$).

availability in the disturbed forest at the landward end of its range, but strongly limited by water stress at its seaward edge. *Cladium mariscus* is a sedge, which explains its higher LMA relative to the other woody species in the study. However, across the communities it occurred, LMA and patterns of stomatal conductance did not significantly differ (Figures 4 and 5), even though the light availability between the communities of *C. mariscus* occurrence was different (Figure 3), suggesting it was not as responsive to light availability as predicted. Additionally, *C. mariscus* had significantly lower predawn (0400) water potentials in the freshwater marsh zone than in its other communities of occurrence (Figure 5), where its midday (1200) water potential became extremely negative before recovering back towards predawn levels as the day progressed. The very negative predawn and midday water potentials suggest *C. mariscus* is under water stress in the freshwater marsh (the seaward edge of its range) and is, therefore, at its physiological limit. In all communities where it co-occurred with *B. halimifolia* and *M. cerifera*, *C. mariscus* had significantly lower midday water potentials (Figure 5). Hence, *C. mariscus* is not as responsive to light as predicted, but water stress, likely due to flooded soils at its seaward edge, appears to be a major factor in this species exclusion from lower elevation sites (Kozłowski and Pallardy, 2002).

We predicted that *B. halimifolia* should be responsive to increased light availability and tolerant of moderate salinity, but should not tolerate very low light levels or waterlogged soils as its distribution expanded landward, with little seaward contraction (Figure 2). This species showed a unique pattern of LMA, midday water potential, stomatal conductance, and xylem vulnerability to cavitation relative to the other two species. As predicted, midday (1200) water potentials were similar in the sparse ecotone and the seep forest (Figure 5), indicating similar water stress at its seaward and landward edges, respectively. At its seaward edge, in the sparse ecotone, *B. halimifolia* had its highest LMA and wood density. This pattern of a relatively smaller leaf surface in the sparse ecotone, coupled with higher stomatal conductance in mid-morning (0900; Figure 5) when humidity is higher, ambient temperatures are lower, and light is high relative to the dense ecotone and seep forest, indicates that this species is not light limited at the seaward end of its distribution. *Baccharis halimifolia* had its lowest LMA and least negative midday (1200) water potentials in the dense ecotone (Figures 4 and 5), which is the midrange site for this species and also where salinity was highest posthurricane (Figure 1). This indicates that *B. halimifolia* can make physiological adjustment to tolerate the salinity conditions. At its landward edge in the seep forest, where it invaded posthurricane, *B. halimifolia* exhibits symptoms of both light and water limitation. Here, *Baccharis halimifolia* LMA was significantly lower than in the sparse ecotone. This morphological response of increasing leaf surface area in a low-light environment (Poorter *et al.*, 2009) suggests that light limitation may curtail additional landward expansion. Additionally, stomatal conductance in the seep forest was rather consistent over the course of the day for *B. halimifolia* (Figure 5), suggesting acclimation to a more variable light environment because open stomata can take advantage of sudden increases in light availability caused by

sunflecks, therefore compensating for overall decreased light levels and assuring a ready carbon supply (Valladares, Allen, and Pearcy, 1997). Interestingly, wood density was lower in the dense ecotone and seep forest, whereas Ψ_{50} became more negative from the seaward edge (sparse ecotone) to the landward edge (seep forest) (Figures 6 and 7). This relationship between woody density and Ψ_{50} is surprising, given that wood density is often associated with resistance to drought-driven embolism (Hacke *et al.*, 2001, 2006; Sperry, 2003; Tyree, Davis, and Cochard, 1994). Overall, however, more negative Ψ_{50} in the seep forest indicates greater cavitation resistance and suggests a physiological adjustment to water stress at the landward edge of its range.

The broad distribution and abundance of *M. cerifera* remained unchanged (Figure 2). Hence, we predicted this species should be less sensitive to decreased light availability than the other two study species and that it should exhibit little or no difference in water stress at its seaward edge relative to its landward boundary. Midday (1200) water potentials, woody density, and Ψ_{50} did not differ among sites for *M. cerifera*, indicating identical water stress and physiological tolerance of water stress in all communities where it occurred, which is consistent with our hypotheses for this species. Stomatal conductance was much lower in the mesic forest for *M. cerifera*, likely a result of decreased light availability because of greater canopy cover (Figure 3 and 5). However, *M. cerifera* LMA was lower in the mesic forest, at its landward edge, indicating a morphological response to decreased light availability by increasing leaf surface area that could compensate for a lower stomatal conductance (Figures 3 and 4; Poorter *et al.*, 2009). Compared to *B. halimifolia*, *M. cerifera* had greater wood density in the dense ecotone and seep forest (Figure 6) and more-negative Ψ_{50} in the sparse ecotone and seep forest (Figure 7), indicating that *M. cerifera* is less limited by water stress than *B. halimifolia* is. Previous studies have suggested that this species adapts to flooding over time (Tolliver, Martin, and Young, 1997), and our results reflect that.

CONCLUSIONS

The identification of plant morphological and physiological responses to environmental changes along a coastal wetland coenocline that are consistent with observed shifts in distribution following hurricanes is an important step in understanding how species may “re-assort” as SLR and storm surges force changes in distribution (Desantis *et al.*, 2007; Prahalad, Kirkpatrick, and Mount, 2012). Overall, two important points emerge from our study. First, increased understanding of physiological profiles of key coastal wetland species has the potential to reveal functional groups of species (Kirkpatrick and Glasby, 1981) that may respond similarly to the effects of climate change. Second, recent research (Snedden and Steyer, 2012) suggests that identifying a few key abiotic parameters has predictive power in modeling changes in species composition in response to SLR.

Studies that define physiological profiles of species that vary in their distributional responses provide a mechanistic understanding for such models that structure coastal wetland plant communities. Understanding the physiological responses of coastal wetland species is important because these areas are

predicted to experience storms of greater intensity because of climate change (Bender *et al.*, 2010). These disturbances can release herbaceous assemblages from the “coastal squeezing” created by woody encroachment (Shirley and Battaglia, 2008). Hurricanes can generate upslope regeneration sites for at least some species to expand their distributions inland (Fruchter, 2012, this study) or produce storm surges that “push” the distributions of species landward, depending on the physiological tolerance of the species in question (McCarron, McLeod, and Conner, 1998; Platt, Joseph, and Ellair, 2014).

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